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SHORT COMMUNICATIONS

Properties of the dynamics of intertidal microphytobenthic biomass

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The short-term variability of intertidal microphytobenthic biomass was characterized by analysing a 30-day time series encompassing two spring–neap tide cycles. Chlorophyll-*a* concentration was measured every day at the beginning and at the end of every diurnal exposure periods. Microalgal biomass exhibited predictible net increases during diurnal exposures due to a positive production-loss balance. In addition, our data series shows that after an environmental disturbance, even though biomass decreased strongly, it converged quickly back to its initial steady-state oscillation pattern. This study supports some fundamental properties of the dynamics of microphytobenthic biomass, as previously predicted in our mathematical model of primary production.

The high level of biological productivity of intertidal mudflats is largely due to microphytobenthos autotrophic activity; the spatio-temporal dynamics of this community is therefore of prime importance. The first theory about this dynamics (Guarini et al., 2000a) predicts daily oscillations of the biomass due to the shift of exposure periods during day-time (the synchronizers). It also states that the transitory phase occurring after a disturbance is short; total biomass converges quickly (in less than 15 days) towards a stable cycle (Guarini et al., 2000b). To investigate these dynamic properties, a sampling programme with a high temporal resolution was undertaken during a one-month period, encompassing two spring–neap tide cycles.

The Aiguillon Bay is situated along the mid-Atlantic coast of France (47°00′N 01°05′W) and is dominated by intertidal mudflats. Microphytobenthic biomass was estimated by quantifying fluorometrically the chlorophyll-*a* (Chl-*a*) concentration in the uppermost one cm of the mud. Five cores (ID. 15 cm) were sampled at the beginning and at the end of each diurnal exposure period (within the same m^2 each day) during 30 successive days (from 10 July to 8 August 2001). Disturbance of the total sampled area was avoided by means of an appropriate spatial sampling plan. Low tide occurred at midday during spring tides while high tide occurs at midday during neap tides. Therefore, during neap tide periods (15–17 July and 29–31 July) two short diurnal exposures occurred per day, early in the morning and late in the afternoon; thus biomass was sampled before and after the high tide to have the average daily level. Total irradiance ($W\,m^{-2}$) and wind speed ($m\,s^{-1}$) were monitored during the same period.

Short-term variations of the Chl-*a* concentration showed a net increase during day-time exposures (Figure 1); values were significantly higher at the end of diurnal exposures than at the beginning (one-tailed paired *t*-test, $P<0.001$). These results confirm previous observations from a shorter time series (Blanchard et al., 1998) which showed that the dynamics of biomass at high frequency was characterized by a series of oscillations due to primary production during low tides and losses during high tides and night exposures, as predicted by our theoretical model (Guarini et al., 2000b). The exception is the decrease occurring on 18 July, likely due to strong rainfalls which washed out the surface.

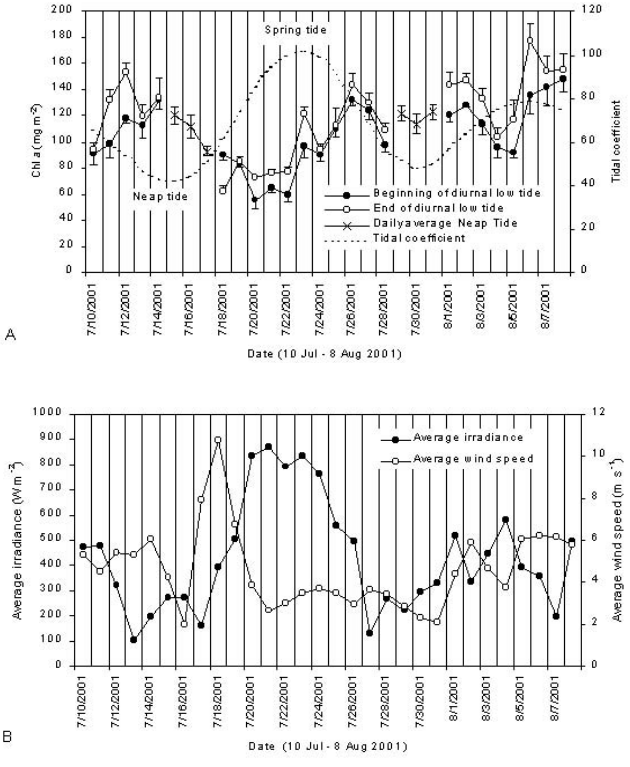

Figure 1. (A) Variation of Chl-*a* concentration in the top 1 cm during 30 consecutive days (from 10 July to 8 August 2001). Symbols represent the biomass level at the beginning of diurnal low tides (filled circles) and at the end of diurnal low tides (open circles) when there was only one complete emersion per day; crosses are the daily average biomass when there were two short emersions per day during neap tides (one early in the morning and the other late in the afternoon). Vertical error bars denote SE. The dotted line indicates the tidal coefficient with neap and spring tide periods. (B) Variation of the average irradiance during exposure (left Y-axis, open circles, $W\,m^{-2}$) and wind speed (right Y-axis, filled circles, $m\,s^{-1}$).

The mean increase of biomass during exposures (i.e. the net community primary production) was 13%, but this estimate was variable (1–34%). This variability encompassed two main components: the first one is deterministic, due to the dynamic variations of the synchronizers within both spring–neap tide cycles. The second one is random and may be due to sampling variability, fluctuations of the forcing variables and local environmental factors. Another source of variability may be attributed to a density-dependent process, as shown by Blanchard et al. (2001): the higher the biomass at the beginning of diurnal emersions the lower the net production.

The dramatic decrease (~ 50%) from 133.12 ±7.90 mg Chl-*a* m^{-2} on 14 July down to 63.77 ±4.31 mg Chl-*a* m^{-2} on 20 July was likely induced by a period of low average irradiance during neap tide (13–17 July; 100–300 W m^{-2}), and was accentuated by a stormy event with heavy rains between 17 to 19 July (average wind speed >6 m s^{-1}) which likely enhanced resuspension into the water column, as demonstrated by de Jonge & van Beusekom (1995) for the Ems estuary. Nevertheless, biomass remained above the minimum level which allows the constitution of a productive biofilm (estimated to about 25 mg Chl-*a* m^{-2}, Guarini et al., 2000a) and ensures that productivity only depends on the photosynthetic activity of diatoms. Under this condition, biomass is expected to converge quickly (in less than 15 days) towards a stable oscillatory set of steady-state values (Guarini et al., 2000b); our observations are in agreement with this prediction as biomass rised back to its initial level (68.45 ±4.19 mg Chl-*a* m^{-2} on 22 July to 137.95 ±4.89 mg Chl-*a* m^{-2} on 26 July) within a few days after the reversal of meteorological conditions (stable anticyclonic conditions from 20 to 24 July). Because our observation period could only report one such disturbing event, it cannot constitute a global validation of this theory; we therefore encourage ecologists to undertake longer time-series to include more disturbing situations so as to document more thoroughly this fundamental property of microphytobenthic biomass, i.e. its ability to converge quickly to a stable steady state. We further suggest that the seasonal pattern has to be studied at this scale of observation since it is characterized by a series of local steady-state cycles which vary in time and space according to the seasonal trend of forcing factors.

Fluctuations around the steady-state values occurred from 26 July onwards (daily means in the range 100.22 ±5.31–156.50 ±11.43 mg Chl-*a* m^{-2}); they were correlated neither to meteorological nor to tidal conditions.

In conclusion, the analysis of this 30-day time series points out two scales of within-month biomass variation: (1) a within-day variability pertaining to the daily exposure increase through primary production (13% in average); and (2) a variability at the scale of several days due to a combination of meteorological and tidal conditions. The former can be predicted while the latter cannot. They represent the nature of microphytobenthic biomass dynamics, as conceived theoretically. The practical consequence of this finding is that it is very difficult to have good estimates of the mean microphytobenthic biomass based on a few samples taken only once a month as it is usually done in annual surveys based on a monthly monitoring (for a review of such estimates see Colijn & de Jonge, 1984). We therefore recommend to take into account these scales of variation to define efficient sampling strategies: sample at the beginning and the end of emersions during two or three successive days, two or three times a month.

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